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ALTERNATIVE EXPLANATIONS FOR EXCEPTIONAL COLOR CLASSES IN DOVES AND CANARIES

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DOVES and canaries have been shown to possess certain color factors which are sex-linked in inheritance. The behavior of these factors leads one to the conclusion that, unlike *Drosophila,* cats and man, the female and not the male is the homozygous sex. In this respect they resemble *Abraxas,* poultry and the domestic pigeon.

In both doves and canaries, however, there occur exceptional color classes in certain matings where the sex-linkage of the factors in question manifests itself. To explain the appearance of these exceptional color classes, Sturtevant (1912) (in canaries) and Bridges (1913) (in doves) have suggested that the principle of *partial sex-linkage* is involved.

Later, Bridges (1916), in discussing the phenomena of *non-disjunction* in *Drosophila,* has reviewed briefly other forms to which he considers non-disjunction may apply and among these mentions doves and canaries as follows:

> (Doves—p. 157) Exceptions to the inheritance of blond and the dark types of pigeons have been explained as partial sex-linkage (Bridges, 1913) but non-disjunction offers an alternative hypothesis which seems plausible.
>
> (Canaries—p. 158) Exceptions to sex-linkage in the inheritance of pink versus black eye colors have been reported (Durham and Marryatt, 1908). These exceptions are explainable by non-disjunction or by partial sex-linkage.

In this paper an attempt will be made to show that the hypothesis of partial sex-linkage and of non-disjunction expect certain results from the crosses made, which have not been reported and in the case of non-disjunction might, in addition, be fairly considered as involving sterility of certain color classes—a phenomenon not yet reported in any of the forms in question.

A further effort will be made to explain the observed facts on an hypothesis of *factorial change* which involves neither a break in sex-linkage nor non-disjunction, and which expects no unusual sterility nor the appearance within the crosses made, of other unrecorded exceptions to the normal relation between phenotypic color classes.

We may take up in order the three hypotheses of partial sex linkage, non-disjunction and factorial change and may compare them on the basis of the experimental results obtained.

Partial Sex-linkage

1. *Doves.*—The normal result obtained when white male and colored female ring doves are crossed, is colored males and white females. This may be explained as follows: Let W equal a factor for the production of colored plumage and w, a factor allelomorphic to it for the production of white plumage. The male is FFMM, the female FFMm in formula. W is linked with M in inheritance.

	White Male wwFFMM	Colored Female WwFFMm
Forming gametes	wFM	WFM and wFm
Zygotes obtained:	WwFFMM = colored males	
	wwFFMm = white females	

In addition, however, exceptional colored females are produced infrequently and have been recorded by Staples-Browne (1912), and by Strong (1912). These exceptional colored females have been acounted for by Bridges (1913), as follows:

> If in the female the sex-differentiating factor and the factor for plumage color are placed close enough together in the same chromosome to be linked, but not so close that linkage is complete "crossing-over" would cause the two factors which entered in the same member of the homologous pair of chromosomes to lie in different members and hence to segregate to different gametes.

If this occurred we should have the following condition:

	White Male wwFFMM ×	Colored Female WwFFMm	
Forming gametes	wFM	WFM	commonly
		wFm	
		wFM	exceptionally
		WFm	
Zygotes formed:	WwFFMM colored male		commonly
	wwFFMm white female		
	WwFFMm colored female		exceptionally
	wwFFMM white male		

This would account for the exceptional colored females, reported from this cross by Staples-Browne and by Strong. It also expects an additional exceptional class—namely white males, and these, though they should occur as frequently as do the colored females, are conspicuous by their absence.

Further than this the hypothesis as just outlined supposes that "crossing over" occurs in the heterozygous sex, between chromosomes which correspond to the X and Y chromosomes of *Drosophila*. This condition has not been observed in *Drosophila* or in forms where a similar opportunity exists and it must therefore, be considered as entirely hypothetical and contrary to such evidence as the most extensively investigated forms have given.[1]

2. *Canaries.*—In this form, the sex-linked inheritance of the factor for dark-eyed color (P) having as an allelomorph pink eye color (p) has been demonstrated by Durham and Marryatt (1908) and reviewed by Sturtevant (1912). Here, however, as in doves there is an unexpected color class which makes its appearance. The exceptional individuals are dark-eyed females which occur in a cross between pink-eyed males and dark-eyed females where only dark-eyed males and pink-eyed females are expected.

Sturtevant, in reviewing the case and in attempting to explain it as the result of partial sex linkage says (p. 570):

This hypothesis could be easily tested. If it is correct, then the cross just discussed should, if large enough numbers be reared, produce as many pink-eyed males as black females." The occurrence of such pink-eyed males has not been reported although it seems almost certain that their appearance in this cross would have been observed and mentioned by breeders did they occur even very rarely.

We may, therefore, say that should the missing color classes appear in the dove and canary matings as predicted by the hypothesis of partial sex linkage, that hypothesis would have a stronger claim to recognition as the correct one for explaining the observed phenomena. Until such time, however, the explanations of the observed exceptions by an hypothesis which requires the appearance of an approximately equal number of exceptions in the same cross, without any evidence that such exceptions exist can not be considered as satisfactory. That this is the case for doves has been suggested by Bridges in his more recent (1916) paper on non-disjunction as already quoted.

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[1] Cole and Kelley (1919) have studied the linkage relations between two sex-linked factors in the domestic pigeon and have on the basis of considerable data, come to the conclusion that "crossing over" occurs in the male but *not* in the female. This result seriously invalidates partial sex-linkage as a possible explanation for the exceptionally colored females in doves or dark-eyed females in canaries. Furthermore, Goodale (1917) has shown that "crossing over" has occurred in the male and not in the female of the domestic fowl—a point which also has a direct bearing on the work with doves and canaries.

NON-DISJUNCTION

In 1916 Bridges, in giving the data on which rests most of the experimental proof of the existence of non-disjunction in *Drosophila,* suggested that the exceptions to sex-linked inheritance in doves and canaries, might be the result of non-disjunction of the sex chromosome.

If, however, the matings producing such exceptional individuals are analyzed on the basis of non-disjunction, certain discrepancies between expectations and actual results become evident. These discrepancies suggest some fundamental difficulties in applying the hypothesis of non-disjunction to the cases in question. Thus if we assume as does Bridges that the sex formula in both doves and canaries is FFMM in the male and FFMm in the female we may represent the crosses made as follows: Theoretically there may be either (*a*) no non-disjunction, or (*b*) non-disjunction in the male, or (*c*) non-disjunction in the female. In each mating we shall consider the three possibilities:

1. In doves:

White Male × Colored Female

	White Male wwFFMM	×	Colored Female WwFFMm
(*a*) If *no non-disjunction;* forms gametes	wFM		WFM wFm
(*b*) If *non-disjunction in the male;* forms gametes	wwFFMM and —		WFM wFm
(*c*) If *non-disjunction in the female;* forms gametes:	wFM		WwFFMm and —

In the three cases the zygotes formed will be as follows:

(*a*) *If no non-disjunction:*

(1) WwFFMM = colored males
(2) wwFFMm = white females

This is the usual result obtained with, however, the addition of exceptional dark females which we are trying to explain.

(*b*) If non-disjunction in the male: forms the following zygotic classes:

(1) WwwFFFMMM = males? Colored? Probably die.
(2) WFM — = colored females? Sterile?
(3) wwwFFFMMm = white males (transmitting non-disjunction).
(4) wFm — = whites? Probably die.

It should be noted that non-disjunction in the male of *Drosophila* does not occur. Yet in pigeons the *male* is presumably the "homozygous" sex and this makes its chromosome condition in respect to sex more closely analogous to the *female Drosophila* in which primary non-disjunction *does* occur. The classes b(1) and b(4) we may fairly suppose, fail to survive. The triple X condition of form b(1) is fatal in *Drosophila* as is the absence of both X and Y seen in class b(4). The two classes b(2) and b(3) are however, real difficulties. The sterility of class b(2), the exceptional colored females has never been reported, as would undoubtedly have been the case, did it exist—just as their appearance alone has excited comment and interest. Class b(3), moreover, would certainly be *white males* and as we have already seen there is no record of any such animals appearing in this cross. Since these white males are the means of transmitting the tendency for non-disjunction to further generations, their presence is necessary for the occurrence of secondary non-disjunction and their absence is a serious handicap to the acceptance of the hypothesis in this material.

(*c*) Non-disjunction in the female:

(1) WwwFFFMMm = colored males (transmitting non-disjunction).
(2) wFM — = white females? Sterile?

It will be seen that the exceptional colored females are neither expected nor explained by this type of non-disjunction. Unless, therefore, we are to assume that non-disjunction in doves is, in almost all its fundamentals, different from the same process in *Drosophila,* producing qualitatively different results, we must agree that it fails to meet the experimental facts. If we do suppose that it differs fundamentally, it may fairly be claimed that no evidence of a conclusive nature either cytological or genetic exists to lead us to say that non-disjunction is in any way involved.

Although the cross just considered is the one chiefly cited, it is of interest to attempt to apply the three possibilities in question to the reciprocal cross namely colored male × white female—as follows:

	Colored Male WWFFMM	×	White Female wwFFMm
(*a*) If no non-disjunction; forms gametes:	WFM		wFM and wFm
(*b*) If non-disjunction in the male, forms gametes:	WWFFMM and —		wFM and wFm
(*c*) If non-disjunction in the female, forms gametes:	WFM		wwFFMm and —

(*a*) No non-disjunction. A normal mating of this type gives two classes of offspring as follows:

(1) WwFFMM = colored males.
(2) WwFFMm = colored females.

No exceptions have been recorded.

(*b*) Non-disjunction in the male: would expect four types of zygotes as follows:

(1) WWwFFFMMM = colored males? Probably die.
(2) WWwFFFMMm = colored males—transmitting non-disjunction.
(3) wFM — = white females? Sterile?
(4) wFM — = whites? Probably die.

Did class b(3), sterile white females occur, their appearance would undoubtedly have been noted and recorded. It should further be noted that non-disjunction, namely in the male, is the only type able to account for the appearance of exceptional colored females in the cross reciprocal to that just considered. In this cross, however, this type of non-disjunction expects a color class which has not been recorded in matings of supposedly homozygous colored males.

(*c*) Non-disjunction in the female:

(1) WwwFFFMMm = colored males transmitting non-disjunction.
(2) WFM — = colored females? Sterile?

Here, non-disjunction gives no exceptions save the occurrence of an occasional sterile colored female. This would undoubtedly be able to escape detection by breeders unless the most careful individual records were kept. However, non-disjunction in the female fails entirely to account for the occurrence of the observed exceptions in the reciprocal cross and may for that reason be disregarded.

Instead, therefore, of increasing the probability that non-disjunction is involved in the production of the exceptions noted, a consideration of the above cross shows that it either fails to account for the exceptions which *do* occur or else expects additional color classes which have not been observed.

2. *Canaries:*

Here the conditions differ but slightly from those already described for doves. The factors involved are P, dark eye color epistatic to p, pink eye color. P is commonly considered as sex linked. The possibilities of non-disjunction remain the same as in doves and may, therefore, be taken up under parallel headings.

Cross of Pink-eyed Male × Dark-eyed Female.

	Pink-eyed Male ppFFMM	×	Dark-eyed female PpFFMm
(*a*) If no non-disjunction; forming gametes	pFM		PFM and pFm
(*b*) If non-disjunction in the male: forming gametes	ppFFMM and —		PFM and pFm
(*c*) If non-disjunction in the female: forming gametes	pFM		PpFFMm and —

The zygotes formed by these three processes would, in order, be as follows:

(*a*) No non-disjunction:

(1) PpFFMM = dark-eyed males.
(2) ppFFMm = pink-eyed females.

It is in this cross that exceptional dark-eyed females sometimes occur.

(*b*) Non-disjunction in the male:

(1) PppFFFMMM = probably dies.
(2) PFM — = dark-eyed females? Sterile?
(3) pppFFFMMm = pink-eyed males transmitting non-disjunction.
(4) pFm — = probably dies.

Here, as Durham and Marryatt who reviewed the case have stated, although canary breeders have long noticed the occurrence of dark-eyed females, *no mention is made of their sterility nor of the occurrence of Class b(3), pink-eyed males, although the latter should have appeared with approximately equal frequency.* When one considers the amount of canary breeding which has been done, and is still being continued and the fact that breeders have long recognized the exceptional dark females; the continued absence of the expected pink-eyed males becomes a real objection to the acceptance of any hypothesis which calls for their appearance.

(*c*) Non-disjunction in the female:

(1) PppFFFMMm = dark-eyed males transmitting non-disjunction.
(2) pFm — = pink-eyed females? Sterile?

It will be noted that this type of non-disjunction fails, as it did in doves, to account for the observed exceptional dark-eyed females.

Further if we now consider the reciprocal cross of dark-eyed male × pink-eyed female, we shall find that the only type (*b*) of non-disjunction which is able to account for the exceptional color class above recorded demands a type of result as yet not reported.

	Dark-eyed Male PPFFMM	×	Pink-eyed Female
(*a*) If no non-disjunction; forms gametes	PFM		ppFFMm pFM and pFm
(*b*) If non-disjunction in the male; forms gametes	PPFFMM and —		pFM and pFM
(*c*) If non-disjunction in the female; forms gametes	PFM		ppFFMm and —

The following classes of zygotes will be expected:

(*a*) If no non-disjunction:

(1) PpFFMM = dark-eyed males.
(2) PpFFMm = dark-eyed females.

No exceptions have been recorded.

(*b*) If non-disjunction in the male:

(1) PPpFFFMMM = dark-eyed? Probably dies.
(2) PPpFFFMMm = dark-eyed males transmitting non-disjunction.
(3) pFM — = pink-eyed females? Sterile?
(4) pFm — = probably dies.

Here it will be observed that pink-eyed females, probably sterile, should be produced as frequently as were the exceptional dark females in the reciprocal cross. We have no evidence that this is the case.

(*c*) If non-disjunction in the female:

(1) PppFFFMMMm = dark-eyed males transmitting non-disjunction.
(2) PFM — = dark-eyed females? Sterile?

Here, as in doves, the result would possibly be masked because no unusual color type is expected. Since, however, this form of non-disjunction would fail to account for the dark females in the cross of pink-eyed male × dark female it may be disregarded.

To sum up, we may say that non-disjunction is able to explain part of the observed facts but expects sterility and other exceptional color classes in crosses where they have not been found. If then, an explanation can be found which expects, in the crosses made, the observed color classes and none other, it should in the absence of stronger evidence for non-disjunction, be considered to be fully as likely an explanation of the phenomena observed.[2]

Factorial Change

1. *In Doves.*—In a paper now in press, I have attempted to show that the occurrence of exceptional color classes in cats (other than tortoise-shell males) which have been variously interpreted as due to partial sex-linkage or to the action of modifying factors, may be satisfactorily explained by a process of factorial change. Thus if in cats in some of the gametes of certain unusual individuals the factor Y for the restriction of black pigment from the coat, appeared in its hypostatic and allelomorphic form y, the exceptional color classes would be accounted for. If a somewhat similar process occurred in certain rare individuals in doves, between factors W and w, but in the reverse direction, namely, from w white to W colored, we should have an explanation for the exceptions observed.

If, then certain white male doves formula wwFFMM formed among their gametes some that were WFM instead of wFM the following result would be obtained in a cross between one of them and a colored female.

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[2] Cole and Kelley (*loc. cit.*) believe that the exceptional colored females in crosses between white male and colored female doves are simply mistakes in observation or records. Because of the fact that they were obtained by two entirely independent investigators and because a similar exception is found in the case of canaries where even more extensive evidence exists, it is believed that the case demands explanation and cannot be merely disregarded as Cole and Kelley imply.

White Male wwFFMM × Colored Female WwFFMm
Forming gametes: wFM commonly — WFM
WFM exceptionally — wFm
Zygotes expected: (1) WwFFMM = colored males (commonly)
(2) wwFFMm = white females (commonly)
(3) WWFFMM = colored males (exceptionally)
(4) WwFFMm = colored females (exceptionally)

Of the two exceptional zygotic classes (3) and (4) only the latter represents a distinguishable phenotypic difference. The other (3) would be merely individuals homozygous for the factor W and therefore indistinguishable, except by proper breeding tests, from the common heterozygous class (1). Such tests have not been reported on as yet by investigators in whose stock, class (4) individuals have appeared. The point to be emphasized, however, is that the presence of homozygous colored males might very easily escape notice unless sufficient numbers of young from a critical cross were raised. It should further be noted that no sterility is expected nor has any been recorded.

If a similar change occurred at rare intervals in certain *white females* as we have a right to expect it possibly would, we should have *no phenotypically aberrant or unexpected color classes formed* in crosses between such females and colored males. We should however, obtain infrequently as a result of this process *homozygous* instead of heterozygous colored males and peculiarly constituted colored females as follows:

Colored Male WWFFMM × White Female wwFFMm
Forming gametes: WFM — wFM, wFm commonly
WFM, WFm exceptionally

Zygotes expected: (1) WwFFMM = colored males
(2) WwFFMm = colored females — commonly.
(3) WWFFMM = colored males
(4) WWFFMm = colored females — exceptionally.

Here again only careful individual breeding tests would be expected to reveal the presence of the exceptional homozygous colored individuals of classes (3) and (4) and no sterility above the ordinary would be expected.

It is also interesting to note that theoretically the colored females of class (4) would when crossed with ordinary white males yield *colored females* of the normal type. Thus:

	White Male wwFFMM	×	Colored Female Class (4) WWFFMm
Forming gametes:	wFM		WFM WFm

Zygotes expected: (1) WwFFMM = colored males.
(2) WwFFMm = colored females.

It may be objected that changes from a hypostatic factor to its epistatic allelomorph are not frequent. This is admitted. On the other hand, they have been several times reported by investigators, among others by Morgan, in *Drosophila,* and by the writer, in mice. In this connection it is interesting to note that the white doves referred to are not totally unpigmented being merely dilute, a fact easily observed in their eye color and found by Strong (1912) to hold true for their plumage.

2. *In Canaries.*—The factors involved are the allelomorphic P for dark eye color and p for pink-eye color. The quantitative relation between the two is somewhat similar to that described in doves though considerably less marked. The factorial change appears to be extremely rare and to be from the p to the P condition. The following results would be expected if the change occurred in the pink-eyed male.

	Pink-eyed Male ppFFMM	×	Dark-eyed Female PpFFMm
Forming gametes:	pFM commonly PFM exceptionally		PFM PFm

Zygotes expected: (1) PpFFMM = dark-eyed males
(2) ppFFMm = pink-eyed females } commonly
(3) PPFFMM = dark-eyed males
(4) PpFFMm = dark-eyed females } exceptionally

Here as in doves the homozygous and heterozygous dark-eyed males would be distinguishable only after a carefully controlled breeding test. The dark-eyed females would be the only exceptional phenotypically distinct color class expected.

If the change occurred in the dark-eyed female instead of in the pink-eyed male we should have the following condition.

Pink-eyed Male × Dark-eyed Female
ppFFMM × PpFFMm
Forming gametes pFM
PFM, pFm } commonly
PFM, PFm } exceptionally
Zygotes expected: (1) PpFFMM = dark-eyed males
(2) ppFFMm = pink-eyed females } commonly
(3) PpFFMM = dark-eyed males
(4) pPFFMm = dark-eyed females } exceptionally

Here again *dark-eyed females* are the only unusual phenotypic color class produced.

In the reciprocal cross we should have the following:

Dark-eyed Male × Pink-eyed Female
PPFFMM × ppFFMm
Forming gametes: PFM
pFM, pFm } commonly
PFM, PFm } exceptionally
Zygotes expected: (1) PpFFMM = colored males
(2) PpFFMm = colored females } commonly
(3) PPFFMM = colored males
(4) PPFFMm = colored females } exceptionally

As in doves the dark-eyed females of class (4) would be expected when crossed with ordinary white males, to produce *dark-eyed females,* an unusual color class, as well as dark-eyed males, a usual one.

It will then be seen that the hypothesis of factorial change accounts for all the observed facts and unlike the hypothesis of partial sex-linkage or that of non-disjunction expects neither exceptional phenotypically distinct color classes as yet not obtained, nor any exceptional degree of sterility.

On the hypothesis of factorial change it should be possible to obtain at rare intervals colored doves from white parents. None of those who reported exceptional colored females have reported this event. Nor have breeders of pink-eyed canaries recorded a dark-eyed bird from a pink-eyed × pink-eyed mating. In neither case, however, have a considerable number of young from such matings been reported by breeders *from animals of the same stock as that which gave the exceptional dark females.* It therefore remains quite probable that such a result could and would be obtained as it was in Morgan's white-eyed flies and in my gray-bellied agouti mice.

Further, it would appear that another possibility, visionary though it may be, exists. If factorial change within a given locus is in any way influenced by other genes or combinations of genes within the cell either during gametogenesis or immediately after fertilization, we should expect that the w or p gene, as the case might be, would be subject to different intra-cellular environment when its allelomorph W or P was present, from that in which it would be placed in a homozygous ww or pp individual. Some of the differences which are bound to exist might well make for its relatively greater instability in the former as compared with the latter case.

Although such a relationship is highly hypothetical, it is suggested that we should be continually on the alert for evidence of possible effects of intergenic and intra-cellular environment as one of the most probable causes of genetic change.[3]

Conclusion

It is believed that the extension of the hypothesis of partial sex-linkage and of non-disjunction, the effects of which have been clearly demonstrated in *Drosophila* should be made to include other forms only after confirmatory genetic and, wherever possible, cytological evidence have been obtained, and in the absence of any other hypothesis which equally fits experimental facts and is capable of experimental proof.

It is therefore suggested that the occurrence of occasional colored females in a cross between white male and colored female doves, and of dark-eyed females in a cross between pink-eyed male and dark-eyed female canaries may be due to a rare factorial change from the factor w to its allelomorph W in doves and from the factor p to its allelomorph P in canaries. Such a change would account for the observed results, except no sterility nor additional unrecorded phenotypes and would be subject to experimental tests.

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[3] It should be recognized that sex-linked inheritance gives opportunity for the recognition of factorial changes should they occur, to a far greater extent than ordinary crosses—for example: In in a case *not* involving sex linkage we cross an individual homozygous or heterozygous for W with a w individual, the small w might change to its epistatic allelomorph W in rare cases without being recognized unless each of the supposedly Ww zygotes resulting from the cross were tested individually and sufficient young obtained to determine whether they are exceptional WW individuals. This has not been done on any very large scale with either birds or mammals under experimental conditions.

If, however, the change occurred in a cross involving sex linkage, it would be at once evident in at least one type of mating. This, as we have seen, is the cross of white wwFFMM male by WwFFMm colored female where any change in the w factor in the male would at once become evident by the production of colored females otherwise not expected.

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